METABOLIC RATES IN SPIDERS

By

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INTRODUCTION

The diversity of spiders is well known in terms of anatomy, behavior, and ecology. These aspects have been documented by Petrunkevitch (1933), Gertsch (1949), and Millot (1949). Although Anderson (1966) studied the excreta of many different spiders, most other physiological studies have dealt with a relatively small number of species. This situation has resulted in a lack of information pertaining to physiological diversity and,as such, precluded a fuller understanding of the biology of these arachnids. I thought that respiration, as measured by oxygen consumption, would be the most productive variable to analyze in this regard, not only because of its ease of measurement, but because it reflects the total energy requirement for all the metabolic processes. This latter point was made by Benedict (1938), and is supported by the wealth of literature where specific physiological processes were studied using some aspect of respiration.

The major aim of this study was to determine whether interspecific differences in oxygen consumption exist and, if so, to uncover some of the causative factors in order to explore the consequences of these differences in relation to the biology of spiders.

Interspecific differences have been detected in a number of arachnids: they have been discovered in oribatid mites by Berthet (1963); in harvestmen by Phillipson (1962); and in scorpions by Dresco-Derouet (1964). In regard to spiders, Derouet (1953) found that a

cavernicolous species had a lower metabolic rate than one which normally lives outside caves.

A second aim of this study was to determine whether being a spider is reflected in an energetic sense by comparing the metabolic rates of spiders with those of other poikilotherms. There is some difficulty in making these comparisons; the weights of the groups being compared often differ, and the relationship between weight and metabolism is not one of direct proportionality. While larger animals have a greater total rate of metabolism than smaller ones, the converse is true when metabolism is put on a per unit weight basis. The relationship between weight and metabolism has generally been represented by the following equations:

$$\text{metabolism} = k \cdot \text{weight}^{n}$$

or

$$\log \text{metabolism} = \log k + n \cdot \log \text{weight}$$

The logarithmic form of the equation is useful since most of the values of n do not equal one, hence an arithmetic plot results in a curved line. A double logarithmic plot of the equation for any value of n does give a straight line. Consequently, to compare metabolic rates, values of n and k are determined from experimental data. The equations represented by these constants can then be compared with one another as well as with standard curves. The latter have been constructed by pooling data obtained from a wide variety of organisms. Examples of such standards are Hemmingsen's (1960) unicellular, poikilotherm, and homeotherm metabolism-weight regression lines.

I also thought it valuable to consider factors which might be responsible for the size of n and k. Hemmingsen (1960) suggested that

the differences between levels of metabolism of poikilotherms and homeotherms, i.e., different values of k, may be the result of an increase in respiratory surface area in the latter group. Tenney and Remmers (1963) demonstrated a relationship between lung surface area and metabolic rate in a group of mammals ranging from bats to whales. In poikilotherms, both Brown (1957) and Hemmingsen (1960) cite data indicating that active fish have larger gill surface areas than sluggish fish of the same weight. Whitford and Hutchison (1967) demonstrated that above 15 C, lunged salamanders have a higher metabolic rate than lungless species of the same weights. These findings indicated the desirability of making interspecific comparisons of the relationship between surface areas of book-lungs and metabolic rates in spiders.

In addition, I thought it of value to investigate metabolic rates of those arachnids having only book-lungs or only trachea. The Solifugae, as most insects, utilize only trachea while the Amblypygi utilize only book-lungs as breathing organs. Thus, knowledge of metabolic rates of solifugids and amblypygids may make comparison of metabolic rates between spiders and insects more meaningful.

In the latest comprehensive review of the subject, Hemmingsen (1960) claims that n, the slope of the metabolism-weight regression equation, equals 0.75 and is quite uniform when large weight and taxonomic ranges are considered. He claims the value of 0.75 has evolved through orthoselection as the result of the struggle between proportionality of metabolism to body weight and to surface functions. Prosser and Brown (1961) and Hoar (1966) presented a more specific hypothesis to explain the size of n. They suggest metabolism is not directly proportional to weight because as animals get larger, a dis-

proportionate increase in supportive tissue is required. This hypothesis assumes that supportive tissues such as the skeleton have low rates of metabolism. I decided to test this hypothesis by assuming that the exoskeleton constitutes the bulk of tissue having a low metabolic rate in spiders.

As a final consideration, the effect of temperature on metabolic rate was studied in order to better evaluate any interspecific differences in metabolism. In general the rates of metabolism of poikilotherms are governed by a logarithmic law relating the velocities of the various component reactions to temperature. However, strict adherance to this relationship is not always followed by poikilotherms. Some variations in the metabolic response to temperature include the temperature compensation response in individuals when exposed to new temperatures as discussed by Bullock (1955), and the relatively new findings of Newell (1966) and Newell and Northcroft (1967) indicating temperature independence to rapid temperature changes in quiescent animals.

With these possibilities in mind, a series of experiments was designed to answer questions about the ability of spiders to remain independent of rapid temperature fluctuations; the ability, degree, and rate of temperature compensation; and the effect of previous thermal history with regard to metabolic rate.

MATERIALS AND METHODS

To increase the probability of detecting interspecific physiological differences, a diverse group of spiders was selected for study. Two species of scorpions were included to aid in comparing spider metabolism with that reported for scorpions by Dresco-Derouet (1964). Adult females were used for the majority of observations as the relative scarcity, short life span, and relatively high activity patterns of males made them unsuitable for study. Immatures of a few species were investigated. The species selected and site of their collection are listed in Table 1.

In general, metabolic rates of poikilotherms are measured under conditions designed to obtain the lowest rate compatible with life when all organs are at minimal levels of activity. Measurements so obtained are termed standard metabolic rates. The conditions used to maintain the arachnids in the laboratory and the conditions under which measurements of standard metabolism were made are described in the following paragraphs.

The arachnids were housed individually in glass containers of appropriate size. Sheets of balsa wood were added to the cages of the web building species and the salticids to provide a framework for webs or the silken retreats of the latter. The cages of the other arachnids were partially filled with moist sand.

The arachnids were kept at a temperature of 20 C except during the

TABLE 1

LIST OF EXPERIMENTAL ANIMALS

Order Family	Species	Collection Site
ARANEIDA		
Ctenizidae	*Ummidia audouini* (Lucas)	Torreya Ravine, Liberty Co., Florida
Theraphosidae[a]	M species	12 miles north of Colima, Colima, Mexico on Highway 110
	H species	5 miles west of Puebla, Puebla, Mexico on Highway 150
	G species	Tehuantepec, Oaxaca, Mexico
Lycosidae	*Lycosa lenta* Hentz	Gainesville, Alachua Co., Florida
Salticidae	*Phidippus regius* (C.L. Koch)	Gainesville, Alachua Co., Florida
	Phidippus otiosus Hentz	Gainesville, Alachua Co., Florida
Filistatidae	*Filistata hibernalis* (Hentz)[b]	Gainesville, Alachua Co., Florida
Theridiidae	*Achaearanea tepidariorum* (C.L. Koch)	Gainesville, Alachua Co., Florida
	Theridion rufipes Lucas	Gainesville, Alachua Co., Florida
	Tidarren sisyphoides (Walckenaer)	Gainesville, Alachua Co., Florida
SCORPIONIDA		
Buthidae	*Centruroides hentzi* (Banks)	Gainesville, Alachua Co., Florida

TABLE 1 (Continued)

Order Family	Species	Collection Site
	Centruroides vittatus (Say)	Alabama ?
SOLFUGAE		
Eremobatidae	*Eremochelis bilobatus* (Muma)	Portal, Arizona
AMBLYPYGI		
Tarantulidae	*Tarantula marginemaculata* (C.L. Koch)	Plantation Key, Monroe Co., Florida

[a]The confused state of taxonomy of this group prevented species determination.

[b]Lehtinen (1967) places this species in the genus *Kukulcania*.

experiments dealing with the effects of temperature change. This temperature was selected because it approximates the average temperature where most of the arachnids were collected. It is also a temperature commonly used in measuring metabolic rates of poikilotherms; thus it facilitates the comparison of data with those of other workers. Relative humidity was kept near 100% by the addition of a few drops of water to the cages at frequent intervals. In addition, a shallow tray of water was kept in the incubator. A high relative humidity was maintained since it was discovered that certain lycosid spiders tended to reduce their oxygen consumption when the humidity was lowered to 10%. In essence, these conditions were used to prevent undue stress on the animals. A 12 hr light and dark cycle was maintained in the incubator with illumination provided by a 40 w bulb or a 40 w fluorescent tube. The arachnids were fed various types of living insects once a week. The purpose of the feeding schedule was to maintain constant body weights. The efficacy of the feeding schedule was tested by monitoring individual weights. Oxygen consumption for the purpose of obtaining standard metabolic rates was measured at 20 C, 100% relative humidity, and at a point of minimal activity. Phillipson (1962) demonstrated temporal variations in oxygen consumption in harvestmen. Phanuel (1967) and Dresco-Derouet (1961) detected patterns in oxygen consumption corresponding to activity cycles in certain salticid spiders and scorpions, respectively. These results pointed to a potential problem of defining the time of day when metabolism should be measured. Consequently the oxygen consumption of a number of species was measured over a 24 hr period at 20 C, 100% relative humidity, and a 12 hr light and dark cycle to find the time of day when the metabolic

rates were consistent with the definition of standard metabolism. Once determined for each species, this time period was used for all subsequent measurements.

Since my definition of standard metabolism depended on the existence and maintenance of a daily rhythm of activity where I could measure oxygen consumption at a time when the arachnids were not active, I thought it valuable to set up a control experiment to detect possible sources of error if the acclimation conditions inadvertently produced a loss of rhythm. Individuals of L. lenta, a species which from field observations and preliminary studies of oxygen consumption was known to exhibit temporal variations in activity and oxygen consumption, were kept under constant darkness at 20 C and 100% relative humidity for three weeks. The oxygen consumption of this experimental group of L. lenta was then measured in the evening, a time when they are normally active in nature. The results were compared with standard metabolic rates of a control group of L. lenta that had been kept at 20 C and 100% relative humidity but under a 12 hr light and dark cycle to see if loss of the temporal pattern of oxygen consumption occurred, and also to see whether the rates of oxygen consumption obtained for the experimental group were comparable to standard metabolic rates for this species.

Observations were made on individuals after they were exposed to 20 C, 100% relative humidity, and the 12 hr light and dark cycle for three weeks. Metabolic rates were not measured on any individual until six days after their last feeding to preclude variations in metabolic rates due to the absorption of food from the gut.

Actual oxygen consumption was measured using a Gilson differential

respirometer. Warburg flasks of about 15 ml capacity were used to house the arachnids in most instances. Some of the larger lycosids and all the theraphosids required the use of 125 and 200 ml flasks. About 0.2 ml of a 10% (w/v) KOH solution was placed in the center wells of the flasks to absorb the expired carbon dioxide. Granular soda lime, (a mixture of NaOH and $Ca(OH)_2$), was used for this purpose in the case of the larger flasks. About an inch of the soda lime was layered at the bottom of the flasks and covered with several thicknesses of plastic screening to prevent contact with the animals. One-half ml of water was placed in the side arms to produce a water saturated atmosphere within the flasks. For those spiders whose oxygen consumption was measured under conditions simulating daylight, 75% of the flask was covered with black plastic tape to minimize the effect of bright light. All measurements were converted to ul of dry gas at 760 mm Hg and 0 C.

An estimate of the respiratory quotient of the arachnids was required to compare oxygen consumption data with data of other workers whose results are reported in kilocalories. This estimate was obtained using P. regius. Twenty-five specimens were placed individually in Warburg flasks as usual except that no KOH was added to the center well. A 30 minute reading was made. Since no KOH was present, any changes in the level of the manometric fluid reflected both oxygen consumption and carbon dioxide production. A second 30 minute reading was made with KOH in the center well. As the expired carbon dioxide was absorbed by the KOH, this second measurement reflected only oxygen consumption. By assuming oxygen consumption was constant for the two 30 minute intervals, I calculated carbon dioxide production and subsequently the respiratory quotient.

Estimates of book-lung surface area were made from measurements of scaled drawings of serial cross-sections of spider abdomens. The histological procedures used were described by Mitchell (1964). The sections were 8 u thick and stained with a Chlorazol black E saturated solution of 70% (v/v) ethyl alcohol. Drawings of sections of a book-lung were made with the aid of a split image drawing tube. Every fifth or tenth section was drawn depending on the size of the spider, hence estimates of surface area and volume were made from 10 or 20% of the total number of sections. The volume of a book-lung was estimated from measurements made using a polar planimeter, while total respiratory surface area was estimated from measurements of individual lamellae in the drawn sections. The lamellae refer to the leaves of the book-lung as they appear in cross-section. Since the spiders investigated have a pair of book-lungs, both volume and surface area values were doubled to provide estimates for the whole spider.

The extent of development of the tracheal systems was obtained by examination of specimens after they had been boiled in a 10% (w/v) solution of KOH.

The relationship between exoskeleton weight and total weight was calculated from data obtained as follows. Live spiders were weighed one week after they had fed. The spiders were killed and the viscera were removed from the exoskeleton by scraping with a scalpel. The contents of the legs were removed by rolling a glass cylinder down the length of the legs so as to force extrusion of their contents from the detached proximal ends. The exoskeleton was dried at 105 C until a constant weight was obtained.

To study effects of temperature, members of a species were kept

at 20 C, 100% relative humidity, and a 12 hr light and dark cycle for three weeks. The metabolic rate was measured at 20 C. The temperature was then changed to 30 C and oxygen consumption monitored until a stable set of readings was obtained. This reading represents the metabolic rate at 30 C after acclimation to 20 C. The spiders were kept at 30 C for six days with oxygen consumption measured daily to detect temperature compensation effects. On the sixth day, after completion of the 30 C reading, the temperature was changed first to 20 C and then to 10 C. Oxygen consumption was measured at both temperatures. The rates obtained at 30 C, 20 C, and 10 C on the sixth day were assumed to represent metabolic rates at the respective temperatures after acclimation to 30 C. The actual time required to effect a temperature change of 10 C varied between 15 to 20 minutes. Once the new temperature had been reached, one to three hours was required to obtain a stable metabolic rate at the new temperature.

The entire procedure was repeated to study acclimation at a temperature of 10 C. Individuals of a species were acclimated to 20 C, 100% relative humidity, and a 12 hr light and dark cycle for three weeks. At the conclusion of the acclimation period, metabolic rates of these individuals were measured at 20 C. The temperature was changed to 10 C and oxygen consumption monitored until a stable metabolic rate was obtained. This reading represents the metabolic rate at 10 C after acclimation to 20 C. The spiders were kept at 10 C for eight days with oxygen consumption measured daily. On the eighth day, after completion of the 10 C reading, the temperature was changed to 20 C and then to 30 C. The spiders were kept at these two temperatures until a stable metabolic rate was obtained. A time interval of one to

three hours was required at each temperature. The rates obtained on the last day at 10 C, 20 C, and 30 C were assumed to represent metabolic rates in response to acclimation to 10 C.

The temperature range of 10 to 30 C was selected as one the animals might normally encounter in nature.

RESULTS

Weight Changes: The results obtained from weight measurements are summarized in Table 2.

TABLE 2

WEIGHT CHANGES IN SPIDERS

Species[a]	Number of Individuals Measured	Avg Original Wt ± SE (mg)	Avg Final Wt ± SE (mg)	Interval Between[b] Measurements Minimum	Maximum
F. hibernalis	23	594 ± 27	537 ± 23	1 week	6 months
L. lenta	13	925 ± 54	943 ± 75	2 weeks	6 months
P. regius	24	577 ± 23	555 ± 24	1 week	2 months
T. rufipes	12	28 ± 2	28 ± 2	2 weeks	1 month

[a]Only mature females were used in this part of the study.

[b]No initial weighings were made until the spiders had been held under acclimation conditions for at least three weeks.

There were no statistically significant differences between average initial and final weights in the species tested. On the basis of this evidence I assumed that the feeding procedures were adequate to maintain a constant body weight in all the experimental animals.

Temporal Variation in Oxygen Consumption: The average oxygen consumption over a 24 hr period is shown in Figures 1 and 2 for individual species. Sample sizes are indicated in each figure. Temporal variation

Figure 1. Oxygen consumption over 24 hours. Each point represents the mean of N determinations. The time interval indicated by the black stripe represents the 12 hour dark period. (a) L. lenta, N = 6; (b) F. hibernalis, N = 14.

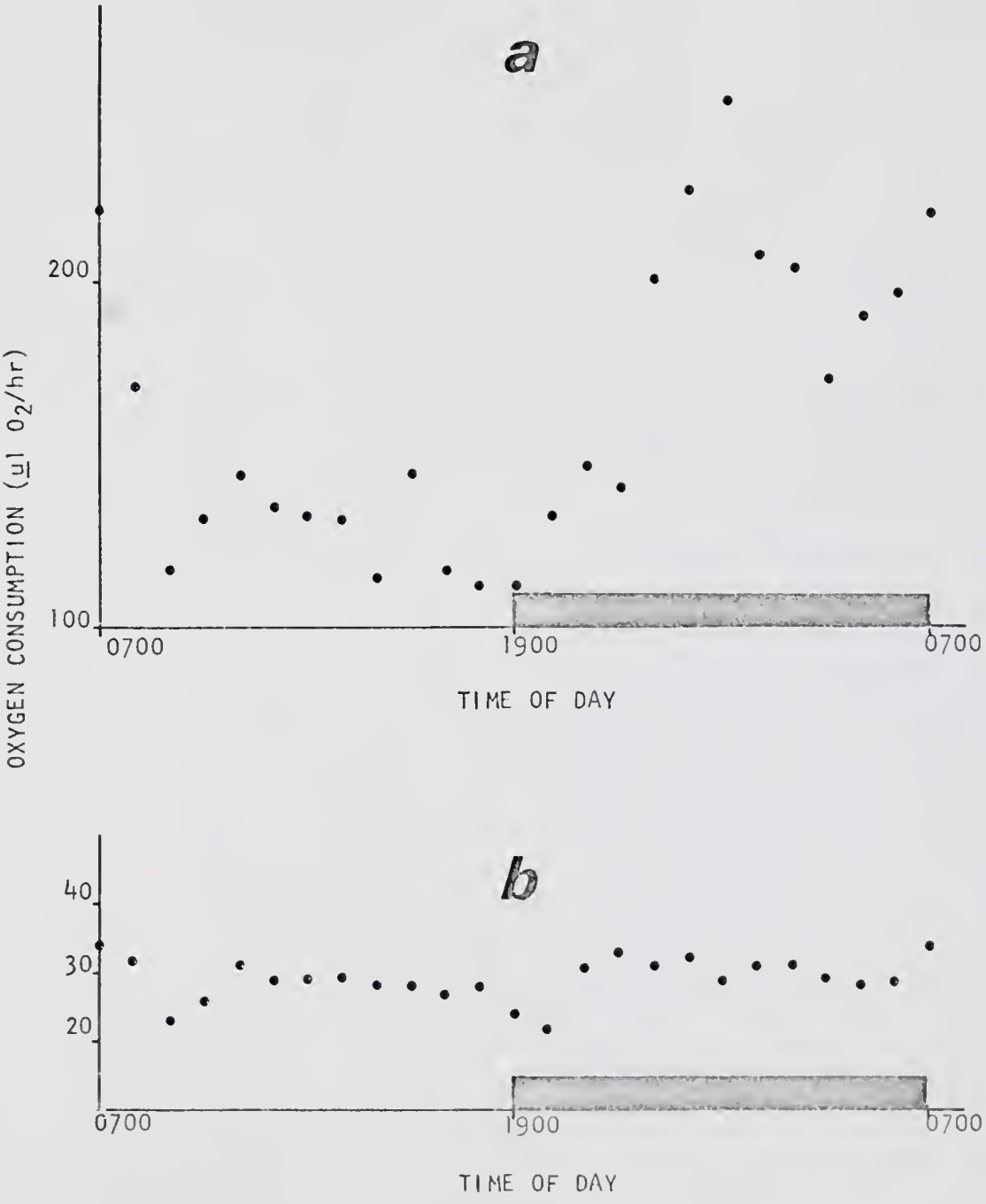
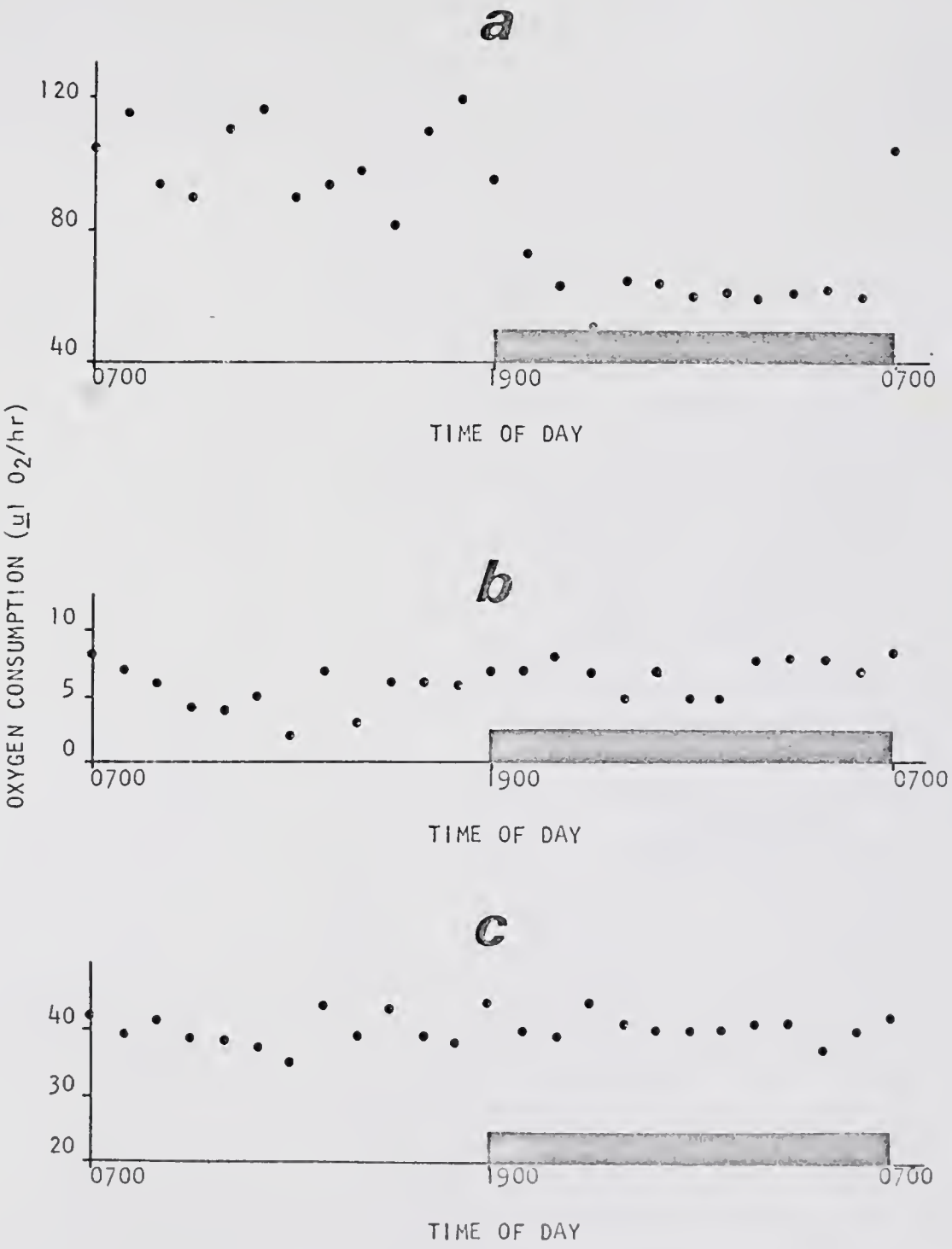

a
200
100
OXYGEN CONSUMPTION (µl O_2/hr)
0700
1900
0700
TIME OF DAY
b
40
30
20
0700
1900
0700
TIME OF DAY

Figure 2. Oxygen consumption over 24 hours. Each point represents the mean of N determinations. The time interval indicated by the black stripe represents the 12 hour dark period.
(a) *P. regius*, N = 6; (b) *T. rufipes*, N = 5; (c) *A. tepidariorum*, N = 5.


a
120
80
40
0700
1900
0700
TIME OF DAY
OXYGEN CONSUMPTION (µl O2/hr)
b
10
5
0
0700
1900
0700
TIME OF DAY
c
40
30
20
0700
1900
0700
TIME OF DAY

was evident for L. lenta and P. regius with the highest rates of oxygen consumption occurring at a time when each species is active in nature. Subsequent measurements for obtaining standard metabolic rates were made in the evening for P. regius and during the daytime for L. lenta when their respective rates reached minimal levels. Temporal variation was not detected in the other species. Their metabolic rates appear to be slightly higher at night, but the variation between the hourly readings and the relatively small magnitude of the rise at night prevented making a firm decision about the existence of a daily pattern of oxygen consumption in these species. Measurements of oxygen consumption over a 24 hr period were not made on the other arachnids. I felt the close correspondence between the patterns of oxygen consumption with the normal activity rhythms of L. lenta and P. regius, as well as a knowledge of the activity cycles of the other arachnids studied, justified measurement of oxygen consumption of the latter group during that part of their activity cycle when physical activity was known to be minimal.

Loss of Temporal Variation in Oxygen Consumption: The control group of 17 individuals of L. lenta that had been exposed to an alternating 12 hr light and dark cycle had a mean standard metabolic rate of 81 ul O_2/gm/hr with a SE of $\pm$ 3. The experimental group of 11 individuals, whose metabolic rates were measured during the evening after they had been exposed to constant darkness for three weeks, had a mean rate of 81 ul O_2/gm/hr with a SE of $\pm$ 6. The correspondence of the metabolic rates of the control group measured during the daylight and the experimental group measured during the evening when members of this species are normally active suggests that constant darkness extin-

guished the temporal variation in oxygen consumption. It also suggests that standard metabolic rates would be obtained even though acclimation conditions extinguished any metabolic rhythm.

Standard Metabolic Rates: The standard metabolic rates of the various arachnids tested are listed in Tables 3 and 4. Individual data are reported in Table 4 since small sample sizes did not make it feasible to pool data in certain species. The relationship between weight and metabolic rate for individual species and various groupings of species has been computed, and the parameters associated with the regression equation that describes the relationship,as well as correlation coefficients,are reported in Table 5.

TABLE 3

AVERAGE OXYGEN CONSUMPTION OF ARACHNIDS AT 20 C

Species[a]	Number of Individuals Measured	Avg Wt ± SE (mg)	Avg Metabolic Rate ± SE (ul O_2/hr)	Avg Wt Specific Metabolism ± SE (ul O_2/gm/hr)
F. hibernalis	81	571 ± 15	29 ± 2	50 ± 2
P. regius	78	568 ± 35	54 ± 2	93 ± 4
P. otiosus	13	337 ± 30	48 ± 5	147 ± 19
L. lenta	80	970 ± 27	90 ± 5	94 ± 5
A. tepidariorum	7	73 ± 11	25 ± 3	356 ± 33
T. rufipes	51	25 ± 1	5 ± 1	201 ± 11
C. hentzi	15	212 ± 18	9 ± 1	43 ± 6

[a]Only mature females were used in this part of the study.

TABLE 4

OXYGEN CONSUMPTION OF INDIVIDUAL ARACHNIDS AT 20 C

Species	Specimen	Wt (mg)	Metabolic Rate (μl O_2/hr)	Wt Specific Metabolism (μl O_2/gm/hr)
T. sisyphoides	14	110	17	155
U. audouini	1	379	14	37
Theraphosid species				
M series adults	M-9	23,120	426	18
	M-10	19,230	420	22
	M-11	22,150	284	13
	M-13	22,500	642	29
M series immatures	M-12	3,600	128	36
	M-15	1,960	49	25
	M-16	5,130	109	21
H series adult	H-77	9,770	262	27
H series immatures	H-75	2,900	71	25
	H-76	4,060	96	24
G series adult	G-2	14,290	317	22
G series immatures	G-9	5,100	198	39
	G-10	2,640	143	54
C. vittatus	CV-1[a]	359	21	59
	CV-2	451	22	49
E. bilobatus	SO-1	63	16	249
	SO-2	109	27	246
T. marginemaculata	T-1	456	19	41
	T-2[a]	290	7	23

[a] males

TABLE 5

CALCULATED SLOPES AND INTERCEPTS OF THE EQUATION LOG METABOLISM = LOG K + n · LOG WT

Sample	Sample Size	Slope (n)	95% Confidence Interval for Slope	Intercept at X = 0 (K)	95% Confidence Interval for Y[a] at $\bar{Y}$	Correlation Coefficient (r)
L. lenta						
immatures	14	0.96	0.77-1.15	-0.8516	1.0874-1.2328	0.95
adults	80	0.85	0.51-1.18	-0.6011	1.8763-1.9487	0.50
total	94	0.87	0.78-0.96	-0.6744	1.7682-1.8326	0.90
P. regius						
immatures	33	0.71	0.59-0.83	-0.3610	0.6846-0.8104	0.91
adults	78	0.73	0.43-1.03	-0.3148	1.6627-1.7351	0.49
total	111	0.77	0.73-0.82	-0.4437	1.3881-1.4441	0.96
F. hibernalis						
adults	81	0.75	0.44-1.06	-0.6424	1.3876-1.4540	0.48
T. rufipes						
adults	51	0.50	0.29-0.71	-0.0246	0.6101-0.7087	0.56
Theraphosids						
total	13	0.78	0.56-0.99	-0.7309	2.1917-2.3553	0.92
All spiders	372	0.70	0.67-0.73	-0.2928	1.4247-1.4673	0.92
All arachnids	393	0.70	0.67-0.74	-0.3231	1.3982-1.4434	0.90

[a]Y = log metabolic rate and X = log wt in mg.

Respiratory Quotient: The average respiratory quotient of 25 individuals of P. regius was 1.02 with SE equal to ± 0.04. On the basis of these measurements, the conversion ratio of 5.05 kilocalories per liter of oxygen was used to convert oxygen consumption values to kilocalories for all the species studied. The conversion made possible comparison of the metabolic rates of the arachnids studied with the data reported by Hemmingsen (1960).

Breathing Systems: Surface area and volume estimates of book-lungs for individuals, as well as a description of the degree of development of the tracheal system on the species level are given in Table 6.

Exoskeleton Weight, Metabolically Active Tissue Weight, and Total Weight: Individual exoskeleton weights, total weights, and estimates of weights of metabolically active tissue are reported in Table 7. The estimates of active tissue weights were obtained by subtracting exoskeleton weights from total weights.

Oxygen Consumption and Temperature: The rates of oxygen consumption obtained at different temperatures are listed in Table 8. Figure 3 provides a graphic illustration of the relationship between oxygen consumption and temperature in P. regius.

The sensitivity of metabolism to temperature change is evident when rates of oxygen consumption at different temperatures within the same temperature acclimation regimen are compared.

The existence and degree of temperature compensation of individuals of a species at a relatively high temperature of 30 C can be determined by comparison of the values obtained at 30 C to acclimation temperatures of 20 and 30 C. All the species tested, except F. hibernalis, show an appreciable reduction in oxygen consumption during a six day

TABLE 6

RESPIRATORY GAS EXCHANGE SYSTEMS OF SPIDERS

Specimen	Percent of Number of Book-Lung Sections Measured (%)	Calculated Volume of Both Book-Lungs (mm^3)	Calculated Surface Area of Both Book-Lungs (mm^2)	Extent of Development of Tracheal System
L. lenta				
#1	11	1.99	273	Poorly developed;
#2	10	3.20	392	restricted to abdomen.
	Avg	2.60	333	
P. regius				
#2	10	1.21	255	Well developed; extends
#3	10	1.40	233	into cephalothorax.
#4	11	1.32	231	
#5	10	2.32	312	
	Avg	1.56	258	
T. rufipes				
#1	21	0.05	11	Poorly developed;
#2	21	0.04	10	restricted to abdomen.
#3	21	0.07	15	
#4	21	0.12	24	
#5	21	0.04	8	
	Avg	0.06	14	
T. sisyphoides				
#1	21	0.24	43	Poorly developed;
#2	21	0.30	54	restricted to abdomen.
	Avg	0.27	49	

TABLE 6 (Continued)

Specimen	Percent of Number of Book-Lung Sections Measured (%)	Calculated Volume of Both Book-Lungs (mm^3)	Calculated Surface Area of Both Book-Lungs (mm^2)	Extent of Development of Tracheal System
A. tepidariorum				
#1	21	0.22	39	Poorly developed;
#2	21	0.19	38	restricted to abdomen.
		Avg 0.21	39	
F. hibernalis				
#1	11	0.81	99	Very poorly developed;
#2	11	1.07	144	probably not functional
#3	10	1.43	184	in gas exchange
		Avg 1.10	142	

TABLE 7

TOTAL WEIGHTS, EXOSKELETON WEIGHTS, AND ACTIVE TISSUE WEIGHTS

Species	Total Wt (mg)	Exoskeleton Wt (mg)	Wt of Active Tissue (Total Wt minus Wt of Exoskeleton) (mg)
Theraphosid species M series	22,000	736	21,264
A. tepidariorum	103	3	100
	74	2	72
	33	2	31
	99	3	96
	34	2	32
	81	2	79
	58	2	56
	88	2	86
	77	2	75
	111	3	108
	110	5	105
P. regius	1,086	74	1,012
	904	97	807
	269	28	241
	91	3	88
	286	26	260
	212	8	204
	52	3	49
	322	37	285
	278	32	246
	581	42	539
	71	5	66
	403	43	360
	311	23	288
	217	18	199
	138	10	128
L. lenta	1,281	109	1,172
	462	29	433
	560	29	531
	811	54	757
	886	63	823
	1,229	68	1,161
	1,092	73	1,019
	1,152	73	1,079
	714	53	661
	1,024	73	951

TABLE 7 (Continued)

Species	Total Wt (mg)	Exoskeleton Wt (mg)	Wt of Active Tissue (Total Wt minus Wt of Exoskeleton) (mg)
L. lenta	25	1	24
	33	2	31
	112	5	107
	137	6	131
	121	7	114
	336	16	320
	141	8	133
	174	11	163
	203	14	189
	100	4	96
	273	21	252
	51	3	48
	72	3	69
	1,049	127	922
	1,144	148	996
	772	103	669
	967	76	891
	1,162	85	1,077
F. hibernalis	30	2	28
	133	8	125
	32	1	31
	110	6	104
	57	5	52
	156	11	145
	164	12	152
	163	6	157
	149	8	141
	375	22	353
	246	15	231
	734	28	706
	295	24	271
	350	27	323
	509	28	481
	437	30	407
	452	21	431
	375	22	353
T. rufipes	13	1	12
	29	2	27
	13	2	11
	25	2	23
	25	1	24

TABLE 7 (Continued)

Species	Total Wt (mg)	Exoskeleton Wt (mg)	Wt of Active Tissue (Total Wt minus Wt of Exoskeleton) (mg)
T. rufipes	40	2	38
	37	2	35
	15	1	14
	32	2	30
	18	1	17
	29	2	27
	30	1	29
	23	2	21
	23	2	21
	24	1	23
	17	2	15

TABLE 8

OXYGEN CONSUMPTION AT DIFFERENT TEMPERATURES

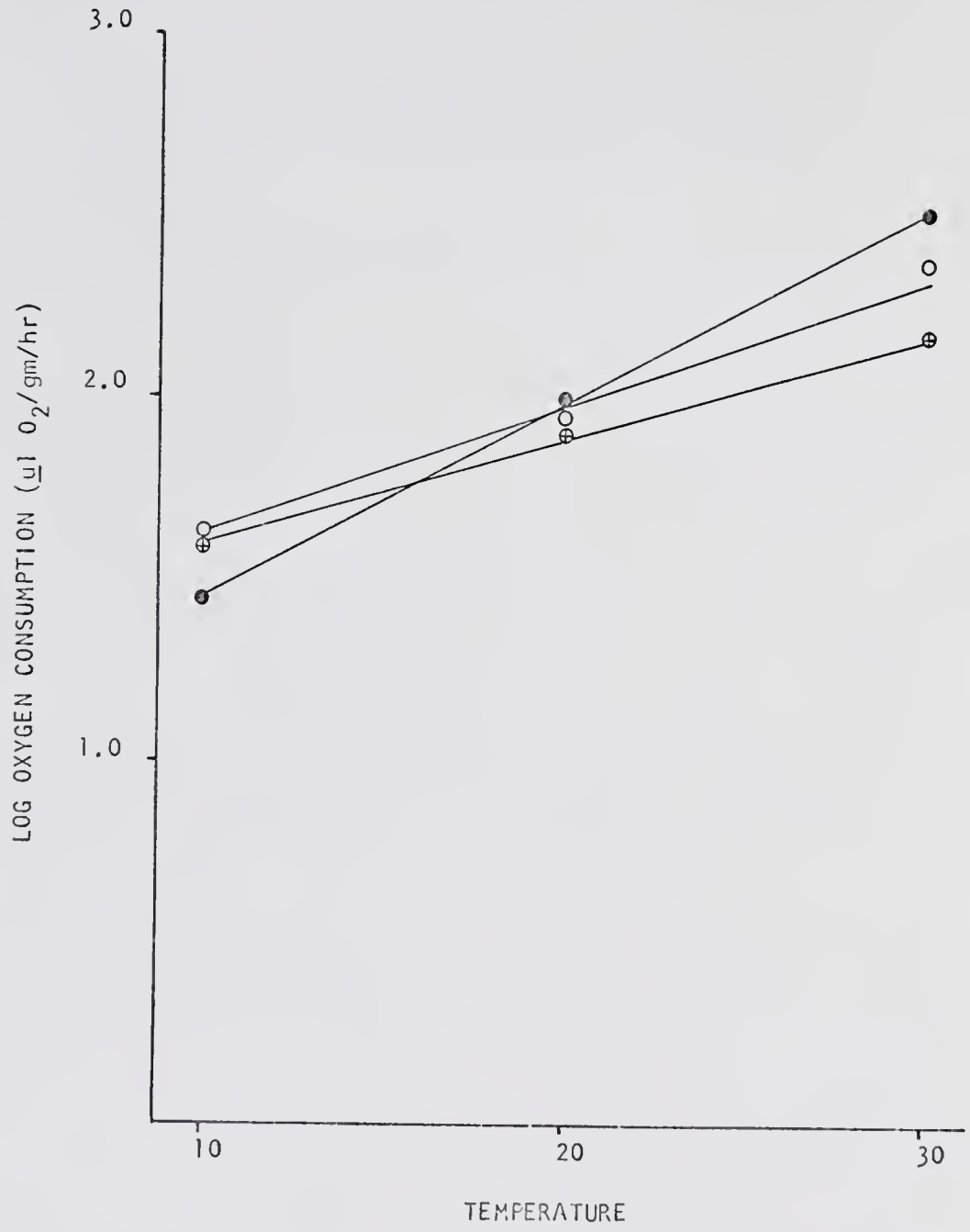
Species	Acclimation Temperature	Length of Exposure	Avg Weight Specific Oxygen Consumption (µl O_2/gm/hr)					
			10 C	N[a]	20 C	N	30 C	N
L. lenta	10 C	8 days	31 (23-39)[b]	14	117 (98-136)	14	240 (220-260)	13
	20 C	3 weeks	28 (23-33)	14	100 (86-114)	50	199 (180-218)	31
	30 C	6 days	26 (21-31)	27	117 (92-142)	27	160 (135-185)	15
P. regius	10 C	8 days	28 (19-37)	14	99 (73-125)	14	329 (273-385)	14
	20 C	3 weeks	43 (34-52)	14	88 (78-98)	42	237 (199-275)	28
	30 C	6 days	39 (29-49)	14	81 (66-96)	14	151 (133-170)	27
F. hibernalis	10 C	8 days	8 (6-10)	11	52 (45-59)	11	144 (129-159)	11
	20 C	3 weeks	25 (21-29)	13	53 (46-60)	41	139 (125-153)	28
	30 C	6 days	19 (16-22)	21	57 (45-69)	25	136 (114-159)	25
T. rufipes[c]	20 C	3 weeks	- - - - - - - - -		149 (101-197)	24	472 (423-521)	27
	30 C	6 days	- - - - - - - - -		168 (139-197)	26	326 (264-388)	26

[a]N refers to the number of individuals measured.

[b]The figures in parenthesis indicate the 95% confidence intervals.

[c]This species was not studied at 10 C. The small size of these spiders and the low temperatures presupposed an inordinate amount of time to measure oxygen consumption at 10 C.

Figure 3. Oxygen consumption of *P. regius* versus temperature. • 10 C acclimation; o 20 C acclimation; ⊕ 30 C acclimation. Acclimation time exposures are indicated in Table 8.


3.0
2.0
1.0
LOG OXYGEN CONSUMPTION (µl O_2/gm/hr)
10
20
30
TEMPERATURE

exposure to 30 C. Statistically significant differences at the 5% level are apparent in the case of P. regius and T. rufipes. The effects of 30 C over time in the metabolic rates of P. regius and F. hibernalis are indicated in Figure 4. Comparison of the oxygen consumption rates obtained at 10 C after acclimation to 10 and 20 C does not reveal any statistically significant increase in oxygen consumption during an eight day exposure to 10 C. In fact F. hibernalis shows a decrease in oxygen consumption indicating a type of inverse compensation. The time course of measurements at 10 C is indicated in Figure 5 for F. hibernalis and L. lenta.

Figure 4. Oxygen consumption at 30 C. Vertical lines represent 95% confidence intervals of the sample means. Spiders were exposed to 20 C for three weeks prior to the start of this experiment. (a) P. regius; (b) F. hibernalis.

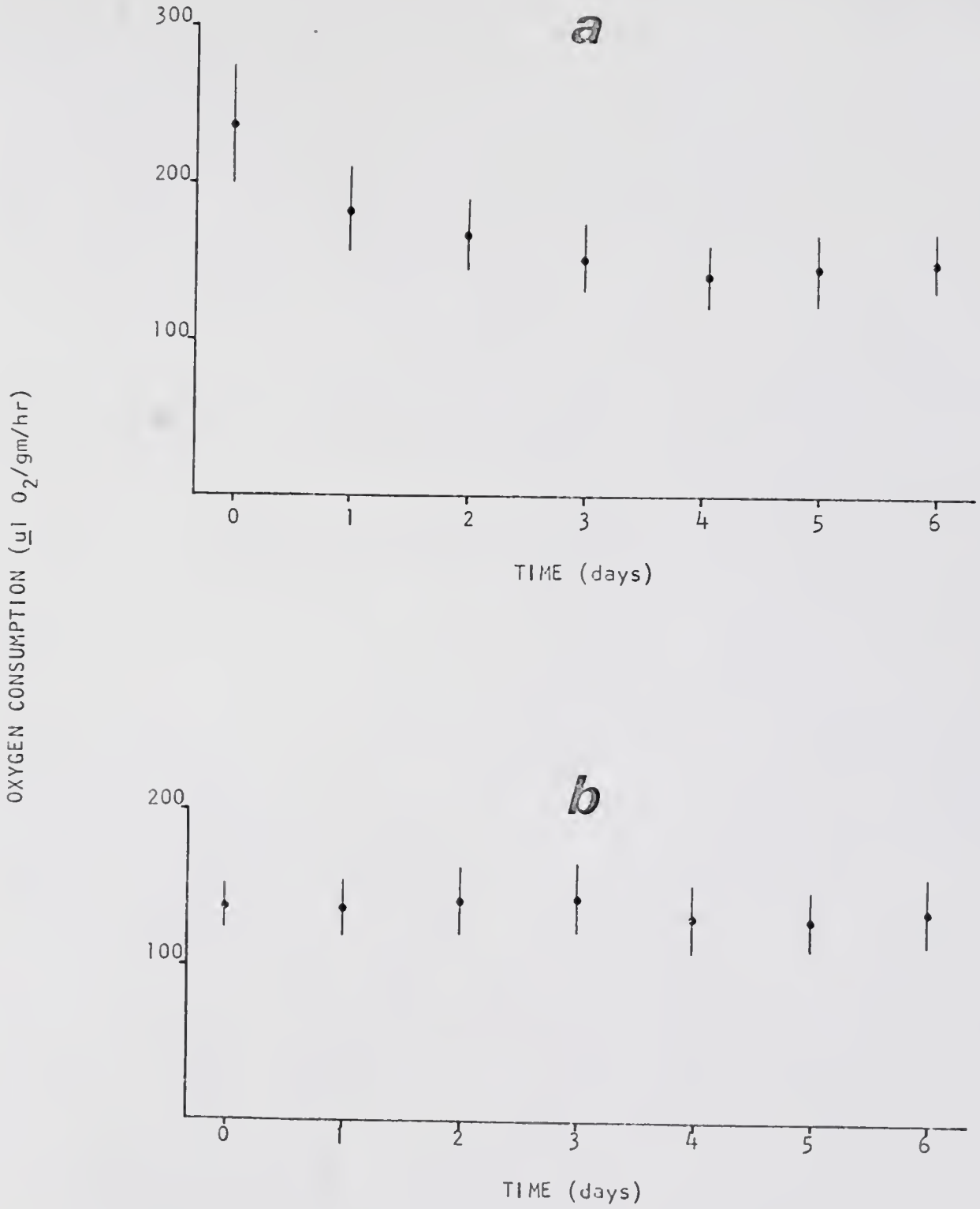
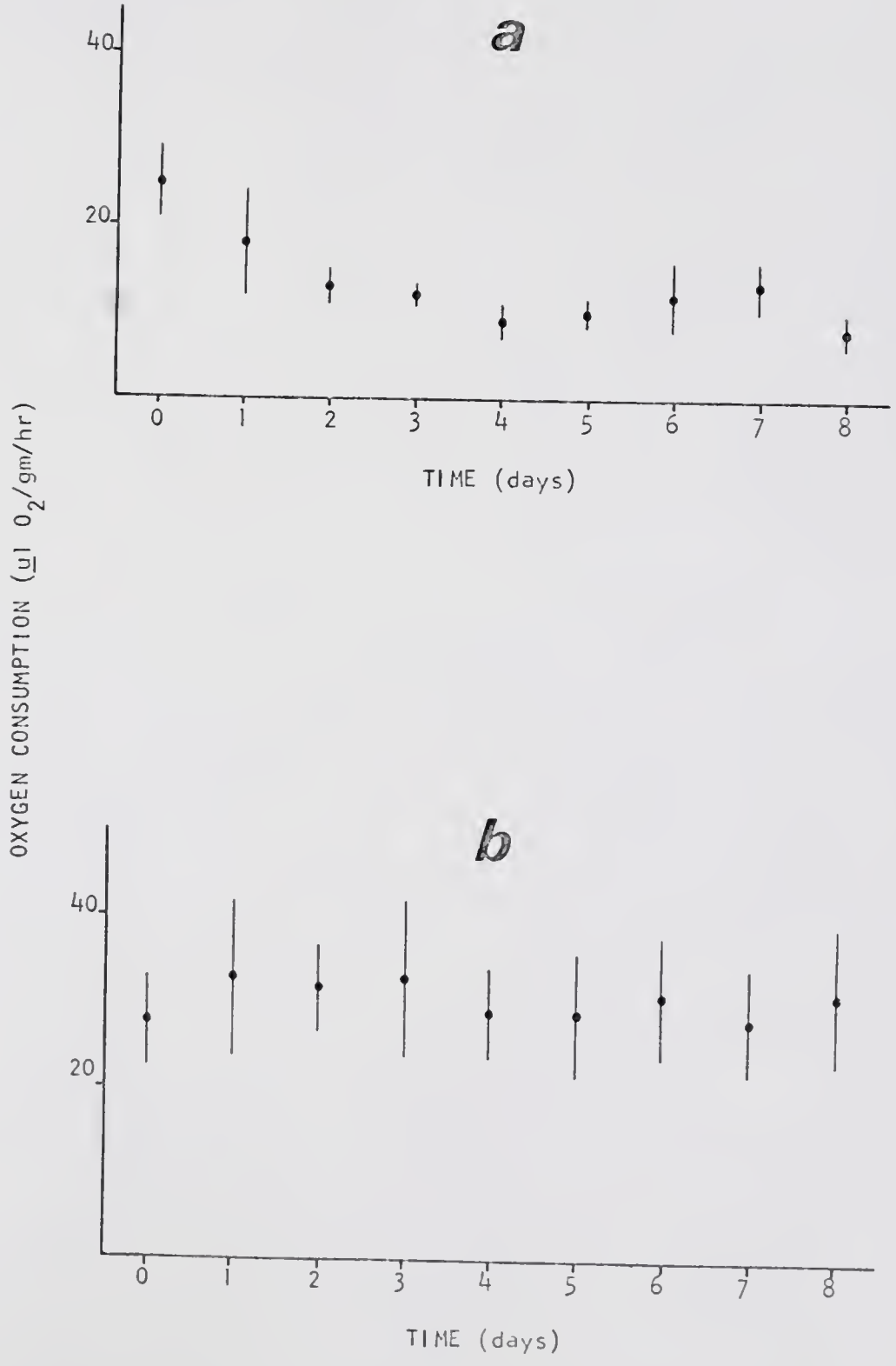

a
300
200
100
0
1
2
3
4
5
6
TIME (days)
OXYGEN CONSUMPTION (µl O_2/gm/hr)
b
200
100
0
1
2
3
4
5
6
TIME (days)

Figure 5. Oxygen consumption at 10 C. Vertical lines represent 95% confidence intervals of the sample means. Spiders were exposed to 20 C for three weeks prior to the start of this experiment. (a) F. hibernalis; (b) L. lenta.


a
40
20
0
1
2
3
4
5
6
7
8
TIME (days)
OXYGEN CONSUMPTION (ul O_2/gm/hr)
b
40
20
0
1
2
3
4
5
6
7
8
TIME (days)

DISCUSSION

Although the study of variation in oxygen consumption over a 24 hr period was conducted for the practical purpose of determining when this measure represented standard metabolic rate, the results have some theoretical import.

Of the five species tested, the two hunting spiders, L. lenta and P. regius, displayed a definite temporal variation in oxygen consumption. Since these observations were recorded over a single 24 hr period, some objection might be made to calling this variation a circadian rhythm. However, studies of oxygen consumption in harvestmen by Phillipson (1962) and those on locomotory activity patterns in salticid spiders reported by Phanuel (1967), where measurements were recorded over two or more 24 hr cycles, support the conclusion that the two spiders have a definite rhythm of oxygen consumption which corresponds to periods of activity in nature. It is doubtful, however, that the measured oxygen consumption of these hunting spiders during their active locomotory phases accurately reflects the oxygen consumption maintained during such phases in nature. While the high rates obtained in the laboratory probably correspond to the time these spiders are active in the field, the magnitude of such measurements may be a reflection of the animals struggling within the confines of a small flask.

Cloudsley-Thompson (1960) suggests the adaptive functions of these

rhythms may partially reside in the avoidance of harsh physical factors. This function is probably of some significance in the case of nocturnal species such as L. lenta. However, the biotic function of synchronizing activity of spiders with the time of greatest prey availability cannot be excluded as a possibility.

A definite temporal pattern in oxygen consumption is not apparent from the results graphed in Figures 1b, 2b, and 2c. The species involved are all web builders; therefore it follows that any rhythmic increases in energy expenditure probably would be associated with building and/or repair of webs. The lack of detection of a rhythm may be an artifact in that the spiders were placed in the Warburg flasks 24 hr prior to measuring oxygen consumption. Webs were built during this time and should have remained in good repair during the course of the experiment.

I am tempted to speculate that the energy spent in the building and maintenance of webs serves the same function, namely prey capture, as that spent during the increased locomotory activity of the hunting species. Certainly the web increases the effectiveness of its owner in sampling the environment for prey, but there may be an added advantage related to energy conservation in those spiders which do not make a new web every day. Once the web is constructed its owner does not have to raise his metabolic rate on a daily basis to insure capture of prey, while hunting spiders must expend energy daily to emerge from their retreats and move about in search of food. Unfortunately this study does not provide data that would support this conjecture for reasons discussed previously.

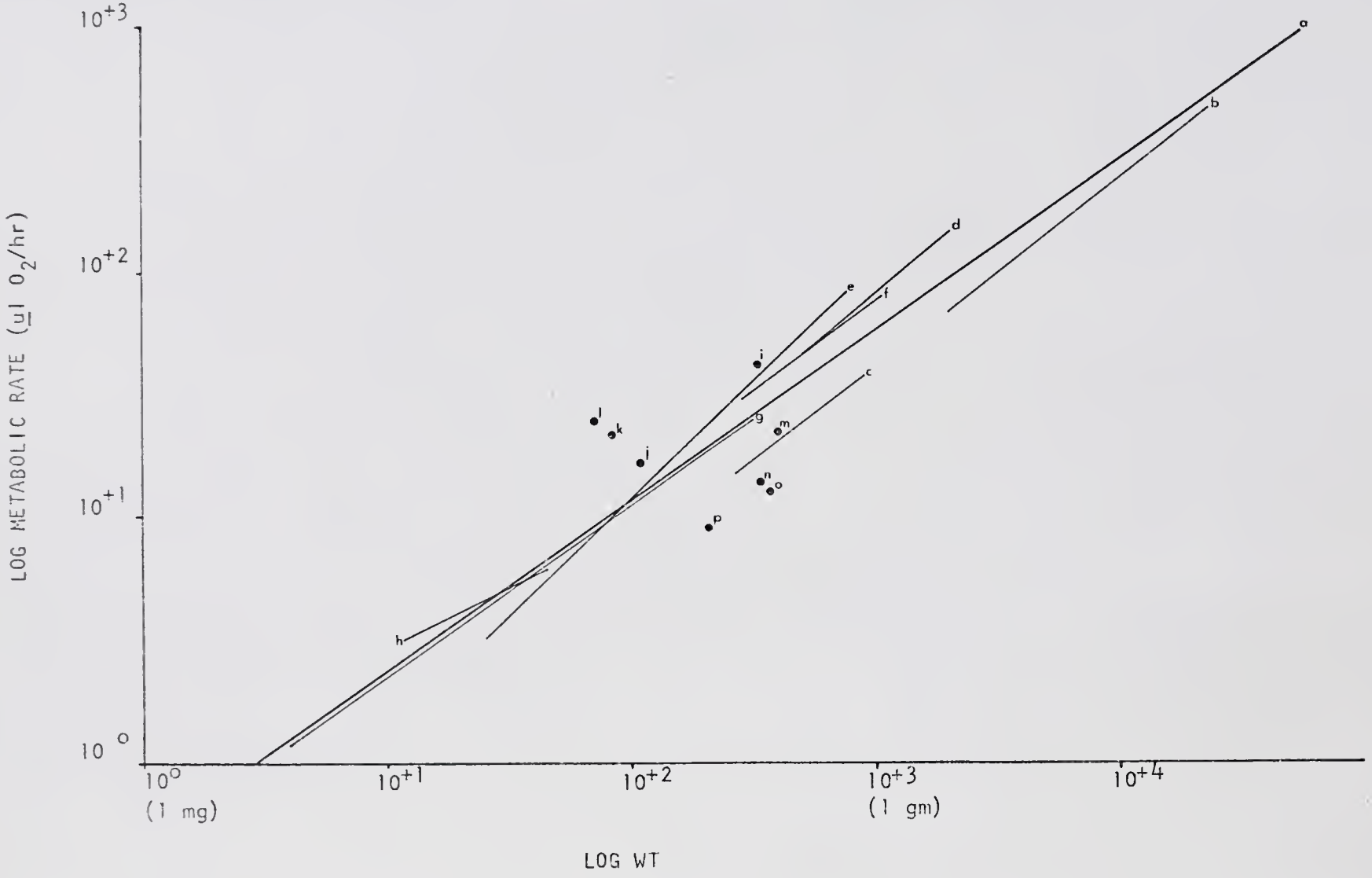
The importance of light as a Zeitgeber was demonstrated by the

correspondence between the standard metabolic rate of L. lenta with the metabolic rate of an experimental group of this species which had been kept in constant darkness. The results also suggest that even though the conditions used to maintain the arachnids in the laboratory extinguished metabolic rhythms, measured rates of oxygen consumption would be compatible with standard metabolic rates. The correspondence of oxygen consumption values obtained under constant darkness with those obtained from organisms when they are in an inactive phase under an alternating light and dark cycle, if substantiated by future research, suggests maintaining organisms under constant conditions to alleviate the necessity of measuring metabolic functions at inconvenient times in order to obtain standard metabolic rates.

To illustrate the interspecific variations in metabolic rates of arachnids, the species metabolism-weight regression lines, and,where appropriate, average metabolic rates versus weights were plotted in Figure 6. In addition, the metabolic rates of all the arachnids were combined and a pooled arachnid metabolism-weight line constructed in Figure 6 as a reference line for the purpose of comparison.

With the exception of one point representing the average metabolic rate of the solfugid, E. bilobatus, all of the values above the pooled arachnid line represent spiders. They include L. lenta, P. regius, P. otiosus, A. tepidariorum, and T. sisyphoides. Immature stages of P. regius and L. lenta as well as adult T. rufipes have metabolic rates which fall on the pooled arachnid line. The values below the pooled arachnid line represent the metabolic rates of the amblypygid T. marginemaculata; scorpions, C. hentzi and C. vittatus; three species of theraphosid spiders; the trap-door spider, U. audouini; and the

Figure 6. Relationship between metabolic rate and weight. (a) pooled regression line for all arachnids; (b) theraphosid species (adults and immatures); (c) F. hibernalis (adults); (d) L. lenta (adults); (e) L. lenta (immatures); (f) P. regius (adults); (g) P. regius (immatures); (h) T. rufipes (adults); (i) P. otiosus (adults); (j) T. sisyphoides (adult); (k) E. bilobatus (adults); (l) A. tepidariorum (adults); (m) C. vittatus (adults); (n) U. audouini (immature); (o) T. marginemaculata (adults); and (p) C. hentzi (adults).


LOG METABOLIC RATE (µl O_2/hr)
10^{+3}
10^{+2}
10^{+1}
10^{0}
10^{0} (1 mg)
10^{+1}
10^{+2}
10^{+3} (1 gm)
10^{+4}
LOG WT
a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p

cribellate spider F. hibernalis. The data on three species of scorpions reported by Dresco-Derouet (1964) agree with the metabolic rate values I obtained for scorpions.

Pooled regression lines were calculated for adult arachnids whose metabolic rates are on or above the pooled regression line and for those whose metabolic rates fall below the line in an attempt to estimate the statistical significance of the difference in metabolic rates of these groupings. Analysis of covariance, as described by Snedecor (1956), was used for this purpose. Unfortunately the slopes of the two lines were shown to be unequal thus preventing further testing of the difference in elevation between the two lines. In a partial attempt to circumvent this problem, the same test was conducted on metabolic rate values of a pair of species, P. regius and F. hibernalis. The metabolism-weight regressions of these species fall above and below the pooled arachnid line, respectively. The suitability of using data obtained from these two species can be seen in Figure 6: their weight ranges and slopes of their regression lines coincide. With 1 and 156 degrees of freedom, the calculated f ratio is 117.74 indicating that the difference between their respective rates of oxygen consumption is statistically significant well beyond the 1% level.

In considering these two groupings, i.e., arachnids with a high or low metabolic rate as evidenced by the position of metabolic rate values in respect to the pooled arachnid line, I came to the conclusion that the various levels of the metabolic rate in arachnids are associated with their evolutionary history, particularly in regards to the fact that arachnids are predators. The arguments leading to this conclusion are developed in the following paragraphs.

The composition of the group with a low metabolic rate includes species that are representatives of primitive orders or are primitive species within a more advanced arachnid order. I use the word primitive in the sense that organisms so described are the most conservative anatomically of their respective taxa. Whether an arachnid was considered primitive or not was made on the basis of information supplied by Millot (1949), Størmer et al. (1955), and Lehtinen (1967). Assuming that physiological conservatism would be correlated with anatomical conservatism, I thought it valuable to discuss the evolution of metabolic rates in arachnids. Since arachnids were one of the first groups to move from an aquatic to a terrestrial habitat, they as predators probably faced the problem of having an inconsistent food supply. A low metabolic rate in this situation would certainly be of value. Even in extant species, a low rate of energy expenditure would be of selective advantage in that it would permit an animal to live in an unstable environment with regard to prey density and/or an environment where the high rate of water loss concomitant with high metabolic rates would be detrimental.

While a plausible argument may be constructed to explain the adaptive significance of a low metabolic rate, the fact that certain arachnids have relatively high metabolic rates deserves some attention. Assuming that during the colonization of the terrestrial habitat prey availability became more and more reliable, the metabolic rates of arachnids could have increased beyond a required minimal level in response to different selective pressures associated with increased activity patterns, rapid rates of development, and increased reproductive potential. I am assuming that these physiological components

require a relatively high rate of energy expenditure and that maximum metabolic rates are a function of standard metabolic rates in the sense that the higher the standard metabolic rate, the higher the maximal metabolic rate. With the exception of the solfugid, the arachnids with relatively high metabolic rates are generally considered to have undergone more evolutionary change than those arachnids with low metabolic rates, at least in so far as the species used in this study are concerned.

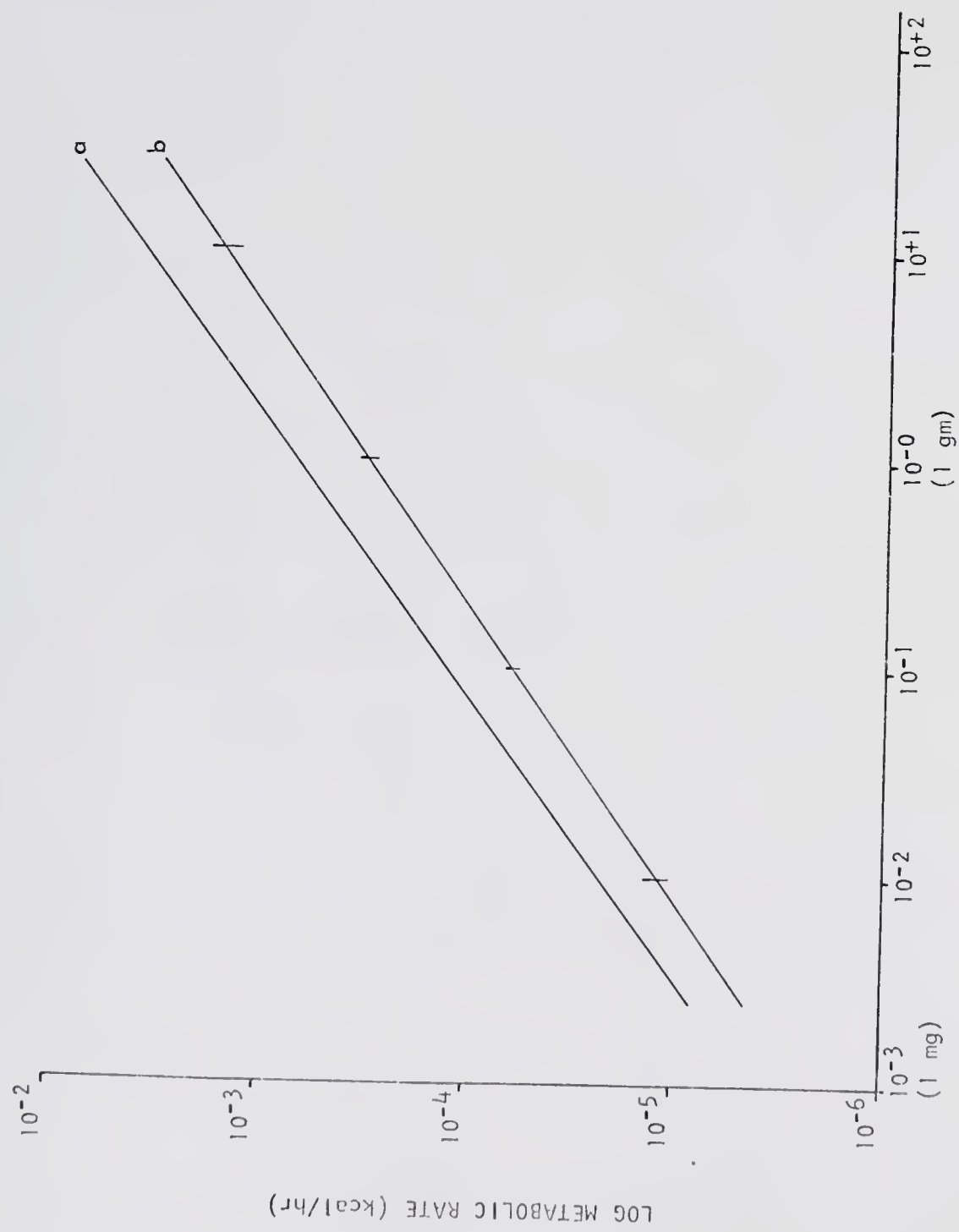
The association of a low metabolic rate with predatory habits and relative lack of evolutionary change is not contradicted by reports in the literature. Harvestmen are not solely dependent on living prey as an energy source and represent one of the most advanced orders of arachnids. A comparison of the metabolic rates obtained at 16 C for two species of harvestmen, as reported by Phillipson (1962), with my pooled arachnid line indicates that harvestmen have a rate of metabolism three to four times higher even though my measurements were made at 20 C. I would argue that harvestmen evolved a relatively high metabolic rate in response to some unknown selection pressure, and one of the requisites of this high metabolic rate is a flexibility in terms of accepting food sources in addition to living prey.

The fact that Dresco-Derouet (1967) reported a low metabolic rate for the harvestman, Ischyropsalis luteipes Simon does not contradict this line of reasoning since this species normally lives in caves. As Frost (1959) points out, one of the main characteristics of a cave environment is a scarcity of food. Derouet (1953) and Dresco-Derouet (1960) also demonstrated that a low metabolic rate is associated with a cavernicolous habitat in spiders.

Hemmingsen's (1960) study was selected as a basis for comparison of arachnid metabolic rates with those of other poikilotherms because of the comprehensive nature of the review. The values of the slopes of the regression equations describing the relationship between weight and metabolism of arachnids, as indicated in Table 5, do not differ significantly from 0.75, a value that has been computed by Hemmingsen (1960) from data obtained from a wide variety of organisms. To detect any difference between levels of metabolism, the metabolic rates of all the arachnids were pooled and then converted to their caloric equivalents. A respiratory quotient of one was obtained from experiments with P. regius and was used to convert oxygen consumption values to kilocalories. The comparison of the pooled arachnid line and Hemmingsen's (1960) standard poikilotherm line is shown in Figure 7. The average metabolic rate of the arachnids sampled in this study is about 40 to 50% lower than that of other poikilotherms over the indicated weight range. I mentioned previously that certain spiders had relatively high metabolic rates for arachnids, however, while these rates approach Hemmingsen's (1960) standard poikilotherm line, they still fall below it. Again I would argue that the low rate of metabolism in the arachnids studied in comparison with other poikilotherms is the result of adaptation to a relatively inconsistent food supply. Further remarks concerning the adaptive significance of high and low metabolic rates will be made below where the results of the effect of temperature on metabolic rate are discussed.

Although the preceding discussion is concerned with the adaptive significance of the various levels of standard metabolism, no mention had been made of the morphological factors which determine the various

Figure 7. Relationship between metabolic rate and weight. (a) Hemmingsen's (1960) poikilotherm line; (b) pooled arachnid line. Vertical lines represent 95% confidence intervals.


a
b
10^{-2}
10^{-3}
10^{-4}
10^{-5}
10^{-6}
LOG METABOLIC RATE (kcal/hr)
10^{-3} (1 mg)
10^{-2}
10^{-1}
10^{-0} (1 gm)
10^{+1}
10^{+2}
LOG WT

rates of oxygen consumption for a given organism. Those arachnids that have metabolic rates above the pooled arachnid line of Figure 6 carry out external respiration by means of book-lungs and/or trachea whereas those arachnids with relatively low metabolic rates utilize only book-lungs for this function. The implication that a tracheal system is a factor associated with a high metabolic rate is supported by certain evidence. The two individuals of T. marginemaculata, which respire by means of book-lungs, had a metabolic rate of 41 and 23 ul O_2/gm/hr while the two individuals of E. bilobatus, which use only trachea, had measured rates of 246 and 249 ul O_2/gm/hr. The spiders that utilize both book-lungs and trachea have a higher metabolic rate than those spiders that utilize only book-lungs. The latter group includes F. hibernalis, a spider having rudiments of a tracheal system. It is doubtful, however, that this system functions in gas exchange in this species. Even the spiders which have a relatively high metabolic rate have rates inferior to those of insects as cited by Hemmingsen (1960). The latter group utilize only trachea. The high metabolic rates of the harvestmen also fit this scheme as they respire solely by means of a tracheal system. This evidence suggests that a tracheal system is more efficient in delivering oxygen to cells than is a book-lung system associated with a circulatory system. However, considering just spiders, the answer is not clear cut. Davies and Edney (1952) demonstrated in the wolf spider, Lycosa amentata, that respiration took place mainly through the book-lungs. Blocking of the spiracular opening of the tracheal system with celloidin did not reduce the oxygen consumption of these spiders. Dresco-Derouet (1960) repeated this experiment on different spiders and obtained the same results. As

indicated in Table 6, P. regius has a well developed tracheal system in addition to book-lungs, yet this spider has a weight specific metabolic rate which closely approximates that of L. lenta, a spider which has book-lungs and a poorly developed tracheal system. The hypothesis advanced by Levi (1967) merits consideration at this point. He suggests the tracheal system is probably important in reducing water loss. As the rate of oxygen consumption increases there is a concomitant increase in respiratory water loss, an intolerable consequence for a small terrestrial organism if not corrected. The trachea may function as a means of reducing this water loss because of a longer diffusion distance and/or smaller spiracles relative to those associated with book-lungs. The one spider with an extensive tracheal system, P. regius, has its highest metabolic rate during the daytime when it would be exposed to conditions conducive to high rates of water loss, i.e., relatively high temperatures and low relative humidities. On the other hand, L. lenta, a spider with a poorly developed tracheal system, is active at night when low temperatures and high relative humidities would not be as conducive to high rates of water loss.

In summary, I suggest that a tracheal system is associated with high metabolic rates because of its efficiency in transporting oxygen, and perhaps more importantly because it reduces water loss. On the basis of experiments of Davies and Edney (1952) and Dresco-Derouet (1960), as well as my analysis of the association between metabolic rates and tracheal systems of P. regius and L. lenta, I concluded that in spiders the tracheal system functions mainly during the active phases of the daily cycle of the spider and not, at least to any great extent, when the spider is quiescent.

If the latter assumption is true, then analysis of the respiratory surface area of only the book-lungs is justified from the standpoint of associating standard metabolic rates with respiratory surface areas. Since estimation of the surface area of a book-lung requires an excessive amount of time, the analysis of the effect of this measure on metabolic rates was conducted interspecifically rather than intraspecifically. Table 9 summarizes the data used in this analysis while Figure 8 shows a graph of metabolism versus respiratory surface area.

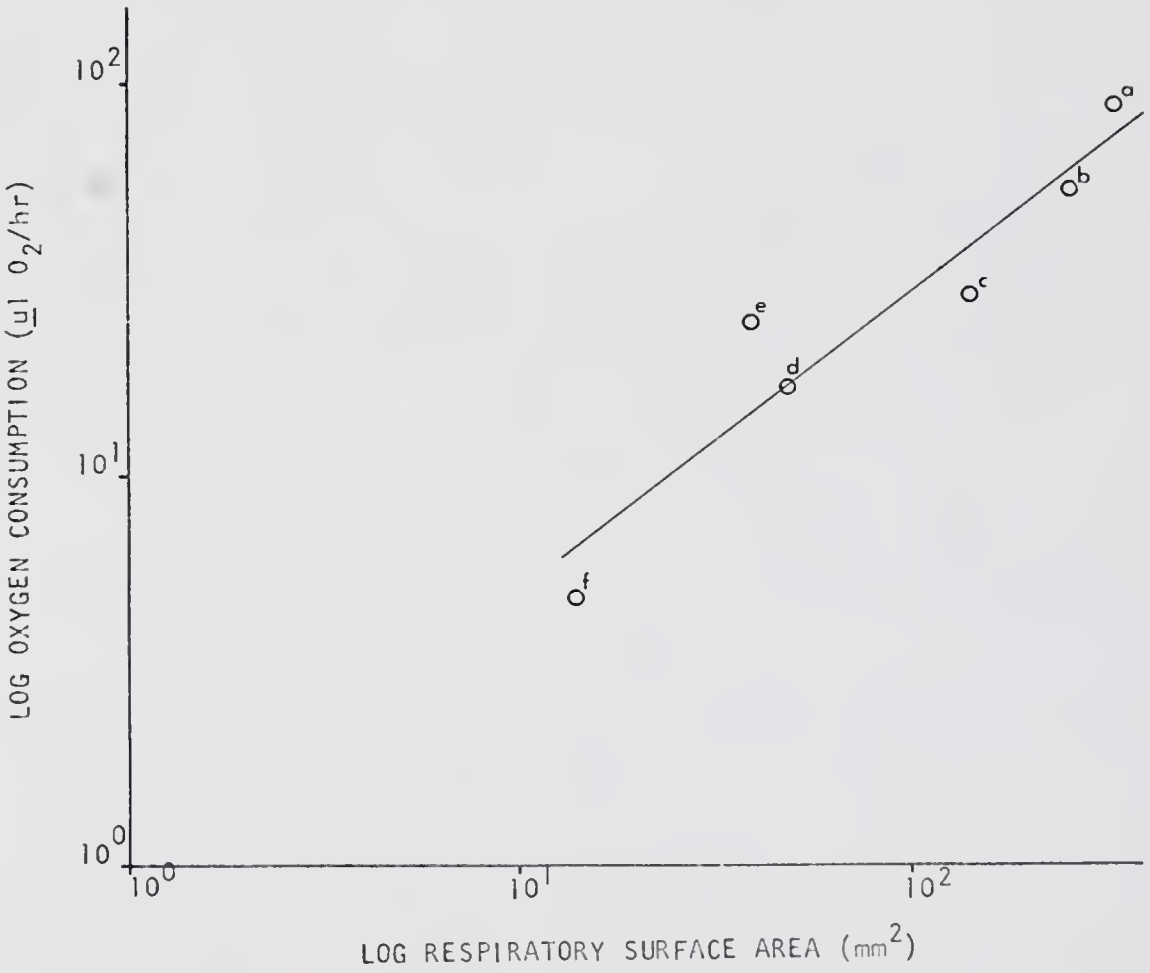
TABLE 9

AVERAGE WEIGHT, METABOLIC RATE AND
BOOK-LUNG SURFACE AREA IN ADULT SPIDERS

Species	Avg Wt (mg)	Avg Metabolic Rate (μl O_2/hr)	Avg Book-Lung Surface area (mm^2)
L. lenta	970	90	333
P. regius	568	54	258
F. hibernalis	571	29	142
A. tepidariorum	73	25	39
T. sisyphoides	110	17	49
T. rufipes	25	5	14

The results listed in Table 9 indicate a general correspondence between metabolic rate and respiratory surface area, i.e., the larger the surface area the higher the rate of metabolism. However, the weight component complicates the analysis as there are only two species, *F. hibernalis* and *P. regius*, which have roughly the same average weight.

Figure 8. Relationship between book-lung surface area and oxygen consumption in spiders. (a) L. lenta; (b) P. regius; (c) F. hibernalis; (d) T. sisyphoides; (e) A. tepidariorum; and (f) T. rufipes.


LOG OXYGEN CONSUMPTION (µl O_2/hr)
10^2
10^1
10^0
10^0
10^1
10^2
LOG RESPIRATORY SURFACE AREA (mm^2)
a
b
c
d
e
f

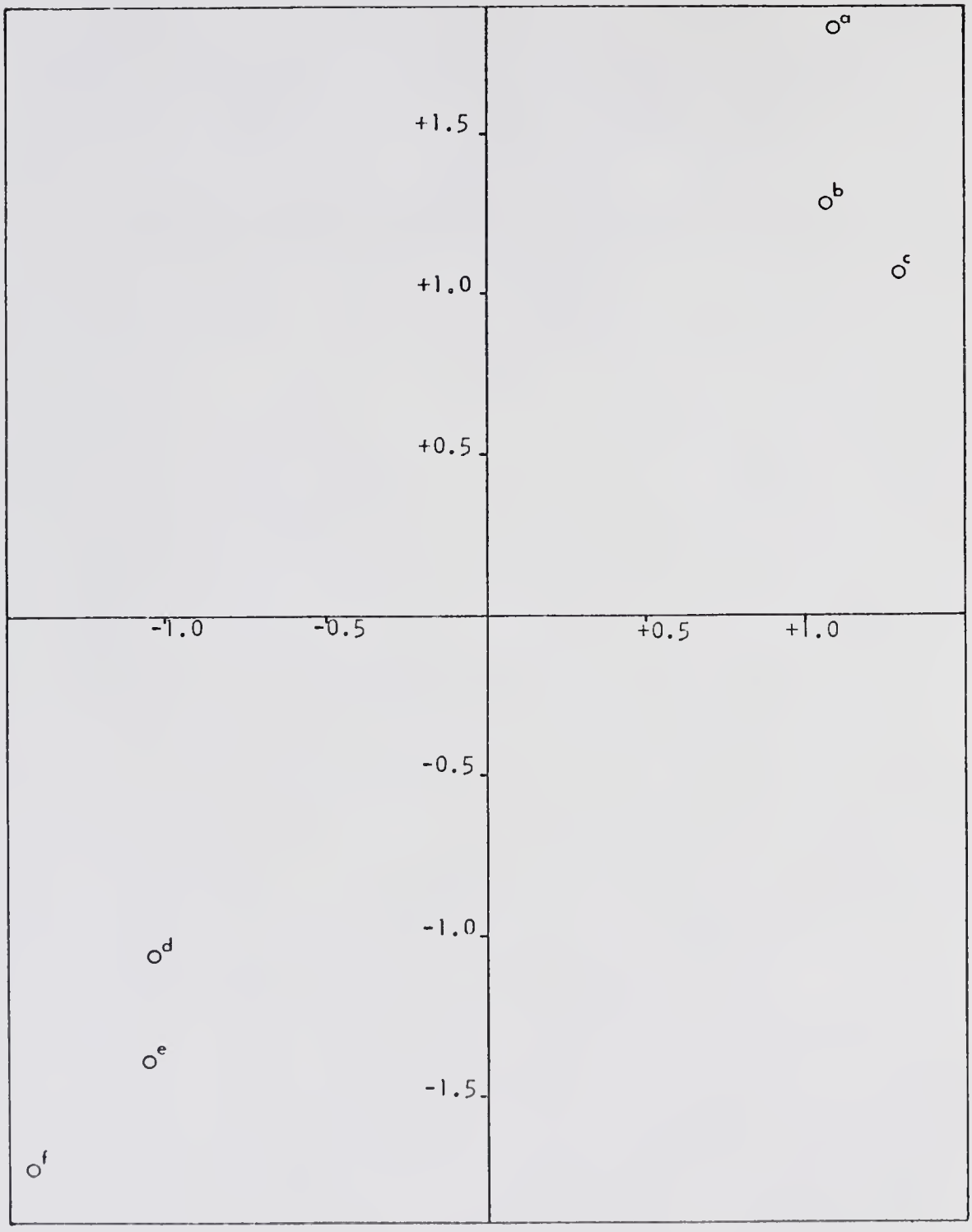
Regression lines describing the relationships of metabolism and surface area to weight were calculated using the average values listed in Table 9 to provide standards in an attempt to correlate deviations in the metabolism-weight relationship with deviations in the respiratory surface area-weight relationship. The logarithemic form of these equations are:

$$\log \text{metabolism} = 0.6320\ (\log \text{wt}) - 0.0408 \quad \text{and}$$

$$\log \text{surface area} = 0.9398\ (\log \text{wt}) - 0.0127$$

The sample correlation coefficients for these relationships are 0.91 and 0.99, respectively. These equations were used to calculate expected metabolic rates and surface areas at the average weights for each species. The calculated values were then compared with the observed values to see whether the deviations between calculated and observed values of metabolic rate corresponded to deviations between calculated and observed values of surface area. The results of these procedures are shown in Figure 9. In every case, where there is a metabolic rate higher than predicted on the basis of the metabolism-weight regression equation, there is a larger than predicted surface area. The converse situation also holds. This analysis suggests that the rate of oxygen consumption is a function of the respiratory surface area of the book-lungs. To ascertain the degree of statistical significance of the relationship between metabolic rate and respiratory surface area, a sample partial correlation was computed. This method of analysis eliminates the effect of weight. The calculated sample partial correlation is 0.86 which, with 3 degrees of freedom, is significant at the 10% level but not at the 5% level. The hypothesis that the greater the amount of surface area the higher the metabolic rate does not imply that other factors such as cardiac output and properties

Figure 9. Deviations of actual versus calculated values of oxygen consumption and respiratory surface area. Abscissa, surface area deviations. Ordinate, oxygen consumption deviations. (a) A. tepidariorum; (b) L. lenta; (c) P. regius; (d) T. sisyphoides; (e) T. rufipes; and (f) F. hibernalis.


+1.5
+1.0
+0.5
-1.0
-0.5
+0.5
+1.0
-0.5
-1.0
-1.5
a
b
c
d
e
f

of respiratory pigments may not be important in regulating the level of oxygen consumption. The former is certainly of some importance since Sherman and Pax (1968) discovered marked variations in heart rate corresponding to levels of locomotory activity in the spider Geolycosa missouriensis.

The hypothesis that disproportionate increases in supportive tissues that occur as animals get larger is responsible for the rate of increase in metabolic rate with an increase in weight is not validated by the results of this study. Regression equations describing the relationships of exoskeleton weight and metabolically active tissue weight to total weight were calculated, and are reported in Table 10. In the case of the three species investigated, the weight of metabolically active tissue increases in direct proportion to total weight, i.e., the slope of the equation describing this relationship approximates a value of one. If the hypothesis were to hold, the slopes of the regressions of weights of metabolically active tissue and rates of metabolism to total weight should equal one another. Comparisons of these values reported in Tables 5 and 10 indicate this is not the case. Unfortunately, the lack of information pertaining to the biochemical composition of spiders precludes testing the assumption that the exoskeleton constitutes the bulk of metabolically inactive tissue. The apparent anomaly where exoskeleton weight increases disproportionally with an increase in total weight while active tissue weight increases in direct proportion, at least in the case of L. lenta, is resolved when these relationships are analyzed. The form of the equations are determined by two variables, namely the slope and the intercept. While exoskeleton weight may increase disproportionally with an

TABLE 10

CALCULATED RELATIONSHIPS BETWEEN EXOSKELETON WEIGHTS
AND METABOLICALLY ACTIVE TISSUE WEIGHTS TO TOTAL WEIGHTS

EQUATIONS: log exoskeleton wt = log K_1 + a·log total wt
and log active tissue wt = log K_2 + b·log total wt

Group	Sample Size	Relationship	Slopes (a and b)	95% Confidence Interval on Slopes	Intercept (log K_1,K_2)	Correlation Coefficient
P. regius	15	exoskeleton wt/total wt	1.20	0.97-1.44	-1.6059	0.95
		active tissue wt/total wt	0.99	0.97-1.00	-0.0006	1.00
F. hibernalis	18	exoskeleton wt/total wt	1.00	0.84-1.17	-1.2473	0.96
		active tissue wt/total wt	1.00	0.99-1.01	+0.0289	1.00
L. lenta	28	exoskeleton wt/total wt	1.17	1.08-1.25	-1.6074	0.99
		active tissue wt/total wt	0.99	0.98-1.00	+0.0002	1.00
Pooled Total[a]	89	exoskeleton wt/total wt	1.05	0.99-1.11	-1.3317	0.96
		active tissue wt/total wt	1.00	0.99-1.01	-0.0225	1.00

[a]The pooled regression was computed from data on species in addition to those listed in this table. Table 7 lists the data used for the pooled regression line. Individual regression equations were not calculated for the additional species because of small sample size or very small weight ranges. These factors prevented computation of regression parameters of value due to the latters' large confidence intervals.

increase in total weight, the mathematical relationship between active tissue weight and total weight can be one of direct proportion due to the higher intercept in the latter. These relationships are indicated in Table 10.

The results pertaining to the effect of temperature on metabolic rate, as recorded in Table 8, indicate oxygen consumption in spiders is not independent of rapid changes in temperature. The calculated average Q_{10} values for temperature ranges of 10 to 20 C and 20 to 30 C are 3.3 and 2.4, respectively. These values are in contrast with the findings of Newell (1966). He claimed the metabolic rates of poikilotherms are largely independent of rapid temperature fluctuations with resulting Q_{10} values ranging from 1.2 to 1.3 provided that metabolic rates of quiescent organisms were measured at frequent intervals. My experimental procedures agree with these requirements in that oxygen consumption was measured at 10 to 15 minute intervals after a rapid 10 C temperature change at a time of day when the spiders were inactive. The correspondence of my results with those of Tribe and Bowler (1968) suggests temperature independence in poikilotherms is not as widespread as Newell (1966) implies.

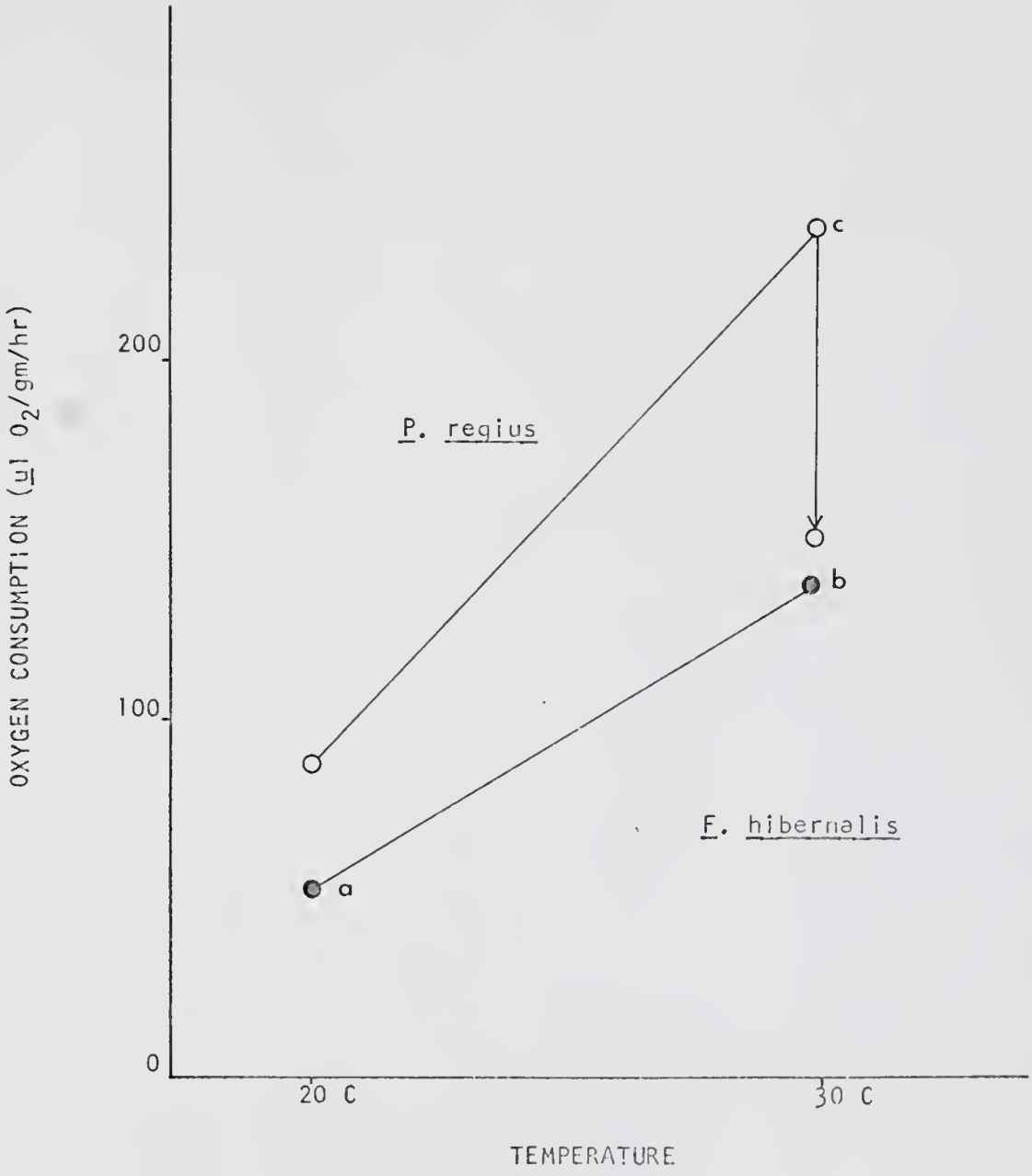
The results recorded in Table 8 indicate previous thermal history does have an effect on metabolic rate when measured at a new temperature. In every case, except F. hibernalis, acclimation to a low temperature of 10 C resulted in a significantly higher metabolic rate at 30 C than would be produced when the spiders were acclimated at 20 C or 30 C. This situation is depicted graphically in Figure 3 where the metabolic rate-temperature curves show a rotation around 20 C. This phenomenon appears to be associated with the ability of individual species to

compensate at high temperatures by lowering their metabolic rates after exposure to the new high temperatures. For example, individuals of P. regius, when acclimated at 20 C for three weeks, have an initial average metabolic rate of 237 ul O_2/gm/hr at 30 C. After a six-day exposure to this temperature, the average metabolic rate decreased to 151 ul O_2/gm/hr. In each case where compensations to a high temperature were detected, the degree of compensation was not complete because the rate of oxygen compensation did not decrease to the level recorded at 20 C. The magnitude of decrease in metabolic rate corresponds to what Precht (1958) terms a 'type 3' compensation. The degree of compensation, computed from the average metabolic rates initially obtained at 30 C after acclimation for three weeks at 20 C and those obtained at 30 C after a six-day exposure to this temperature, involve reductions of 20% for L. lenta, 36% for P. regius, and 31% for T. rufipes. In all cases, the maximal compensation was reached by the third day of exposure to 30 C.

In trying to relate the findings of the temperature studies to standard metabolic rates, I noticed the spiders which showed a decrease in oxygen consumption during exposure to 30 C all had relatively high metabolic rates at 20 C as indicated in Figure 6. The one spider which did not demonstrate compensation at 30 C had a relatively low metabolic rate at 20 C. This correlation suggests homeostatic potential in regards to temperature is perhaps limited by the relative rate of metabolism. Making the assumption there is a certain minimum level of energy expenditure required to keep arachnid protoplasm in a healthy state, it seems reasonable to have a standard metabolic rate at this relatively low level under certain conditions. As mentioned previously, I suspect

the movement from an aquatic to a terrestrial habitat that arachnids made in the geological past presented the problem of a limited food supply. However, as time passed and more and more organisms colonized the terrestrial habitat, the luxury of a high metabolic rate was not selected against, on the contrary it probably possessed certain adaptive adjuncts. One of these adjuncts may relate to the relatively large temperature fluctuations inherent in a terrestrial environment. Consider a spider that has a low metabolic rate at an intermediate temperature. This animal is living close to its minimal level of required energy expenditure. A rise in environmental temperature of 10 C, through its effects on the kinetics of enzyme systems, would result in roughly two fold increases in both minimal and standard metabolic rates. Since the new minimal and standard metabolic rate approximate one another in this case, any reduction in energy expenditure, which might well be desirable from the standpoint of the limitation of energy resources, would be incompatible with maintaining life. On the other hand, a spider with a relatively high metabolic rate at the intermediate temperature, that is to say its standard metabolic rate is appreciably above minimal requirements, when exposed to a higher temperature would also increase its required minimal and standard metabolic rates. However, since this new rate would be above minimal requirements, a decrease in oxygen consumption could take place. This reduction in energy expenditure would be advantageous when the amounts of food required to support the different levels of metabolism are considered. This model is depicted graphically in Figure 10 using the data obtained from F. hibernalis and P. regius. I must admit that this explanation is speculative. The major difficulty stems from the acceptability of

Figure 10. Relationship between temperature and standard metabolism in *P. regius* and *F. hibernalis*. (a) minimal required energy expenditure at 20 C; (b) minimal required energy expenditure at 30 C; (c) compensation at 30 C in *P. regius*.


OXYGEN CONSUMPTION (ul O_2/gm/hr)
200
100
0
P. regius
F. hibernalis
a
b
c
20 C
30 C
TEMPERATURE

the assumption that there is a certain minimal level of energy expenditure which may be different in certain cases from that defined as the standard metabolic rate.

The lack of compensation to the 10 C temperature is not surprising. As predators of insects it would be of little value for spiders to increase their metabolic rate at low temperatures since the low temperatures would also reduce the activity of their prey. I would even suggest that the inverse compensation exhibited by F. hibernalis, a web builder, reflects an adaptation to the greater inhibitory effect of low temperature on flying versus walking insects.

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BIOGRAPHICAL SKETCH

John Francis Anderson was born July 25, 1936, at Hartford, Connecticut. He graduated from Bulkeley High School in June, 1954. From 1954 until 1958, Mr. Anderson served in the United States Marine Corps. Following his release from active duty he entered Central Connecticut State College at New Britain, Connecticut, where he received his Bachelor of Science degree with honors in June, 1962. In September, 1962, he entered the Zoology Department at the University of Florida where he received his Master of Science degree in April, 1965. He continued graduate studies toward the degree of Doctor of Philosophy at the University of Florida while serving as a research and teaching assistant.

Mr. Anderson is married to the former Marjorie Ann Barrett. He is a member of the American Society of Zoologists and Sigma Xi.

This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council, and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December, 1968

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6400 .3.